**The Origin and Behaviour of Chiasmata, IX.
Diploid and Tetraploid *Avena***

by

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In normal meiosis chromosome association at the first metaphase follows the formation of chiasmata in the paired threads at pachytene. In polyploids the multivalent associations formed depend on the occurrence of exchanges amongst the paired chromosomes at pachytene so that, at different parts of its length, one chromosome may be paired with two or more of its homologues. If then chiasmata are formed in these variously associated segments, groups of three, four or more chromosomes remain paired. The mechanism by which large ring associations arise in diploid structural hybrids is the same except that in these the exchanges of partner at pachytene are fixed and obligatory and the resulting associations at metaphase correspondingly more limited in variation.

I have described in detail two types of quadrivalent found in auto-tetraploid plants. The first was that in which little movement had occurred in the chiasmata between diplotene and metaphase owing, as I say, to the weakness of the localised charge inferred at the spindle attachment. This condition was found in *Hyacinthus orientalis*. The second was that in which complete terminalisation occurred. In the early stages the various kinds of chiasmata relationship of *Hyacinthus* were found. At later stages these had been replaced by exclusively terminal association owing to the strong localised repulsion driving the chiasmata away from the spindle attachments to the ends where they fuse. The forms of quadrivalent resulting from this complete terminalisation fall into ten possible types in organisms with non-terminal spindle attachments. (Darlington 1932, fig. 32). This condition was found in *Primula sinensis*.

An important group of organisms including all the cereals so far studied (*Zea*, *Triticum*, *Secale*, and *Avena*) is intermediate between *Hyacinthus* and *Primula* in having a moderate localised repulsion which determines the movement of the chiasmata during terminalisation towards characteristic equilibrium positions in which the proximal spindle-attachment loops merely expand at the expense of the distal loops, so as to be two or three times their diameter, without telescoping them entirely.

Fig. 1. The seven bivalents of the diploid in side view of first metaphase. The total and terminal chiasma numbers are given under each bivalent and the total for the whole complement to the left. $\times 1600$.

The study of these equilibrium positions, first described in *Stenobothrus*, is of interest as showing most clearly the distribution, distance-effect, and relative strength of the forces at work on the chromosomes. Quadrivalents in an organism with the equilibrium types of terminalisation must provide a further test of these conditions, for amongst the configurations to be expected are some with spatial relationships of the spindle attachments and chiasmata such as are not found in bivalents. The material for this study was kindly provided for me by Dr. I. Nishiyama. It consists of two plants:—1.) A diploid F_6 plant from the cross *Avena barbata* ($4x$) by *A. strigosa* ($2x$). The plant is necessarily almost homozygous. 2.) An auto-tetraploid plant derived from tetraploid seed of the diploid F_3 in-bred for three further generations (*cf.* Nishiyama, 1930). The pollen mother cells of these plants were fixed in iron aceto-carmin.

In the diploid (fig. 1) the bivalents resemble those in *Triticum* and *Secale*. 35 bivalents in 5 nuclei had a mean chiasma frequency of 2.57 (total) and 1.66 (terminal).

In the tetraploid (fig. 2) about two thirds of the chromosomes form quadrivalents, the rest usually bivalents. Occasionally univalents are found as in other auto-tetraploids (e.g. *Primula sinensis*

and *Campanula persicifolia*) a situation which probably results from the spatial difficulties of changing partners amongst the chromosomes at pachytene and a consequent incompleteness of pairing.

Fig. 2. The complement of the tetraploid to correspond with fig. 1. Three quadri-valents and eight bivalents. $\times 1600$.

The terminalisation is of the intermediate type and the quadri-valents correspond with the bivalents so far as the simpler configurations are concerned. Where terminalisation is complete the configurations are of the types already described in *Datura* and *Primula sinensis*. There are ten such types allowing for all the possible exchanges of partner at pachytene and eight of these have been found together with instances of incomplete terminalisation which would give these types if complete. In the other two types only incomplete instances have been found (fig. 3, types 12 and 19).

In the simpler configurations the position of each chiasma is governed by the repulsions between the loops on either side of it and in these only two chromosomes are effectively concerned (e.g. types 11 and 17). The situation is more complicated in other configurations (e.g. types 12, 13, 15, and 18). This can best be illustrated by considering the fifth figure of type 13. (figs. 3 and 4). Here an exchange of partner has occurred amongst the chromosomes in the middle of an arm so that each of two chromosomes has formed chiasmata with two others in the *same* arm—proximally two chiasmata, distally a third. In a bivalent the distal one of the two proximal chiasmata would always be terminalised; in the quadri-valent it is not. The repulsion between the spindle attachments of the third and fourth chromosomes has thus prevented the terminalisation of chiasmata between the first and second. As expected on the electrostatic theory of terminalisation the behaviour of the chromosomes is not individual but is governed by the mechanical properties

Fig. 3. Explanation, see p. 132 bottom.

of the whole configuration in which they take part. The same property is shown by the third and fourth figures of type 18. Further in the type 12 figure it appears that the asymmetrical repulsion between the spindle attachment of one chromosome and the body of another has acted to prevent complete terminalisation of the distal chiasma.

Fig. 4. Diagram showing the chromatid structure of certain quadrivalents illustrated in fig. 3 and numbered accordingly. Triple chiasmata in 15(4), 16(2). Quadruple chiasma in 19.

On purely *topological* grounds it can be stated that a chiasma between one chromosome and another cannot be terminalised past a chiasma between one of them and a third: if such a movement is possible on *mechanical* grounds the first chiasma will be arrested and a triple interstitial chiasma will arise. Since such a chiasma has not yet been observed it seems that the conditions of repulsion make an interstitial fusion of this kind impossible.

Fig. 3. Quadrivalents of the tetraploid in early and late metaphase classified according to the ten possible types (11-20) that they would give with complete terminalisation an example of which is given first in each type except 12 and 19. Cf. Darlington, 1932, fig. 32. $\times 1600$.

The great variety of quadrivalent forms provide a means of studying the forces at work in deciding the orientation of the chromosomes on the spindle. From the consideration of multiple rings in interchange heterozygotes I have concluded that each chromosome will separate from the ones nearest it owing to the repulsion being strongest between them provided that (1) a prior incompatible orientation between one of them and a third has not been made (the process not being simultaneous in different parts of the ring) and that (2) the configuration is sufficiently flexible owing to the chiasmata being terminal or the chromosomes very slender.

The *Avena* quadrivalents bear on these conclusions in two ways. First, it will be noticed that all the intimately united configurations lie lengthwise in the axis of the spindle, not equatorially as is often found in *Hyacinthus*. The result must be that the most closely associated pairs will pass to the same pole. I am inclined to attribute the difference to a greater crowding of the chromosomes on the plate in *Avena* than in *Hyacinthus*; this would lead to a greater equatorial repulsion between the different configurations in *Avena* and hence make an axial orientation the more usual equilibrium position.

Secondly, it will be seen that where two pairs are united by terminal chiasmata so as to give a quadrivalent consisting of a series of loops separated by interstitial chiasmata, as in the third figure of type 18, the whole figure behaves like a bivalent not only in respect of the sizes of the loops—the two with spindle attachments being larger—but also in respect of the orientation of successive loops which come to lie at right angles. Thus, when one spindle attachment, separated from another by only a single interstitial chiasma, comes to lie axially as in the fifth figure of type 18, then the second loop is prevented by the rigidity of the chromatids from assuming itself an axial orientation. The internal rigidity of multiple configurations therefore limits the effectiveness of forces which normally determine chromosome movements.

The behaviour of the *Avena* quadrivalents thus bears out the conclusions on chromosome movement before and during metaphase arrived at from the study of simpler configurations. It also provides a basis for interpreting the quadrivalents observed in polyploid species, mutants, and hybrids in *Avena* and *Triticum* where the relationship of the pairing chromosomes is to be inferred from the forms of the configurations and the frequency of their occurrence.

Summary

The quadrivalents formed by an autotetraploid *Avena* are of all the ten possible types. The equilibrium positions of their chiasmata are influenced by the spindle-attachment repulsions of chromosomes not taking part in them. The axial orientation of two members of a quadrivalent can be suppressed by that of the other two owing to the rigidity of the chromatids at an interstitial chiasma between the first two. These observations bear out the mechanical principles inferred from simpler configurations.

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